ÖGH Herpetozoa
Austrian Herpetological Society

Herpetozoa 38: 97–102 (2025)
DOI 10.3897/herpetozoa.38.e139307

The Balkans in Central Europe: a case of introduced lineage of *Podarcis muralis* in Slovakia highlighting the impact of international trading and climate change

Daniel Jablonski[1], Martin Raffaj[1], Dušan Senko[2]

1 *Department of Zoology, Comenius University in Bratislava, Ilkovičova 6, Mlynská dolina 842 15, Bratislava, Slovakia*
2 *Institute of Botany, Plant Science and Biodiversity Centre, Slovak Academy of Sciences, Dúbravska cesta 9, 845 23 Bratislava, Slovakia*

https://zoobank.org/32408BFA-0218-49CA-83A4-BDF568E3220F

Corresponding author: Martin Raffaj (raffaj5@uniba.sk)

Academic editor: Christoph Leeb ♦ **Received** 15 October 2024 ♦ **Accepted** 5 April 2025 ♦ **Published** 19 May 2025

Abstract

This study presents the first genetically confirmed record of an introduced population of *Podarcis muralis* in Slovakia, specifically in the village of Imeľ (southwestern Slovakia, Komárno District), in the Danubian Lowland. The population was likely introduced via the horticultural trade from the western Balkans. It was identified at a horticultural site specializing in the sale of Mediterranean plants from Albania, with individuals of all age stages documented since its initial observation in 2020. Mitochondrial DNA analysis revealed distinct haplotypes that closely cluster with those from northern Albania, indicating clear genetic differentiation from native Slovak populations. This finding was further supported by a species distribution model, which suggested that the Danubian Lowland does not offer a suitable environment for the presence and reproduction of native Slovakian populations. In contrast, a spatial similarity model found environmental similarities between the Danubian Lowland and parts of the western Balkans (northern Albanian lowlands and southern Montenegro). This introduction highlights the role of international trade in facilitating the spread of non-native species, posing potential risks such as hybridization with local populations. With a warming climate, conditions may increasingly favour the establishment of such introduced populations. Thus, regular monitoring is essential to evaluate the implications of these findings for conservation and to safeguard native genetic diversity.

Key Words

Albania, climatic change, hybridization risk, introduction, Lacertidae, native population

Introduction

The common wall lizard, *Podarcis muralis* (Laurenti, 1768), is a well-known species that naturally inhabits much of southern, central, and western Europe, as well as northwestern Anatolia (Speybroeck et al. 2016). This widespread species consists of several phylogenetic lineages that likely began diverging around 6 million years ago (Yang et al. 2022), with further expansion into northern regions toward the end of the Pleistocene. However, its range has been significantly altered by numerous artificial or semi-artificial, human-mediated introductions during the Anthropocene. These introductions have brought the species from southern parts of its natural range into northern areas (e.g., Michaelides et al. 2015) and even beyond Europe (Allan et al. 2006). This has resulted in a complex distribution pattern, creating uncertainty about which populations are native (autochthonous) and which are introduced (allochthonous) (Schulte et al. 2008, 2011; Jablonski et al. 2019; Santos et al. 2019).

As a result, several studies have focused on determining whether such suspect populations are the result of human-mediated introductions or natural but previously overlooked dispersal events, especially at the species'

Copyright *Daniel Jablonski et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

distributional edges (Schulte et al. 2011; Jablonski et al. 2019; Santos et al. 2019; Kolenda et al. 2020; Oskyrko et al. 2020, 2022). These studies have revealed both patterns, natural and human-mediated dispersal. Interestingly, even populations that represent autochthonous lineages in Central Europe may have been introduced by humans to new locations of the region (see discussion in Jablonski et al. 2019). The species' adaptability, which allows it to thrive in new territories or survive transportation, likely plays a key role in its successful introductions of the species to new areas (Wirga and Majtyka 2015).

In Central Europe, allochthonous and introduced populations have been reported in Austria, Germany, and Poland (Schulte et al. 2008, 2011, 2012; Salvi et al. 2013; Kowalik et al. 2025), though they are expected to be present in other countries of the region as well (Funk and Vlček 2023). The origin and population affiliations of *P. muralis* have mostly been revealed through mitochondrial DNA (mtDNA) data, which serves as an effective first step. A recent study on the populations of *P. muralis* in the Czech Republic and Slovakia confirmed only native populations belonging to haplogroup I of the mitochondrial Central Balkan clade (CB) sensu Schulte et al. (2011) and Salvi et al. (2013) (Jablonski et al. 2019). Similarly, a study from Poland confirmed the presence of the same clade, although the authors suspect this lineage may have been introduced, even though natural origin cannot be ruled out (Kolenda et al. 2020). However, in Poland, populations of *P. muralis* with different origins have been now discovered too, showing different ways of introductions, including building materials transportation (Kowalik et al. 2025).

In Slovakia, *P. muralis* is relatively widespread, with some distribution gaps in lowland areas and high mountains (Lác 1970; Lác et al. 2017). Based on mtDNA data, several closely related haplotypes of the CB clade have been found in Slovakia, suggesting recent population isolation and possible colonization of widespread areas (Jablonski et al. 2019). Interestingly, a more localized, distinct haplotype of the CB clade has been found along the Danube River, which may reflect the combination of natural and human-mediated spread, possibly via shipping along the Danube River (fig. 2 in Jablonski et al. 2019). However, all populations of *P. muralis* in Slovakia are now considered phylogeographically autochthonous.

Material and methods

This report aims to highlight a case of *P. muralis* introduction, likely facilitated by recent trade between the Balkans and Central Europe. On 14 August 2023, we were informed about the presence of *P. muralis* in a previously undocumented area in Slovakia, specifically in the village of Imeľ, located in the Danubian Lowland (47.9000°N, 18.1489°E, 110 m a. s. l.). This area is characterized by flat terrain and is influenced by the water regime of rivers, especially the Danube and its tributaries. The local population was discovered at a horticulture site specializing in the sale of Mediterranean and other plants, mainly sourced from northern Albania. The area covers approximately 2,200 m², consisting of rocky and garden sections, and since the first observation of lizards in 2020, all life stages have been recorded, indicating a large and reproducing population.

We visited the site several times, confirming the presence of adults, subadults and juveniles. On June 25, 2024, we collected tissue samples (13533-4) for DNA analysis from two individuals, which were also photographed for the morphological evidence. Moreover, we used two available tissue samples from northern Albania for comparison, i.e. from Shkodër (2808) and from Theth (3152). DNA extraction and laboratory processing of the tissue samples followed the protocol described in Jablonski et al. (2019), i.e. using amplifications and sequencing of mitochondrial DNA (mtDNA), particularly cytochrome *b* (cyt *b*). The newly obtained sequences were deposited to GenBank under accession numbers PQ868063, PQ868064 and PV030916, PV030917.

For the phylogenetic analysis, we start with BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi) to identify *P. muralis* sequences with high similarity to the newly generated sequences, referencing datasets from Salvi et al. (2013) and Jablonski et al. (2019). This analysis yielded 36 sequences from the Balkan Peninsula and Slovakia (Suppl. material 1), which were incorporated into a Maximum Likelihood tree using IQ-TREE (Nguyen et al. 2015) via its online web interface, W-IQ-TREE (Trifinopoulos et al. 2016). The best-fit model was automatically selected by ModelFinder (Kalyaanamoorthy et al. 2017), as implemented in IQ-TREE. Branch support was assessed with 1000 replicates using the Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT; Guindon et al. 2010) and the Ultrafast bootstrap approximation algorithm (UFBoot; Minh et al. 2013).

To highlight the genetic distance between native *P. muralis* populations in Slovakia (Central Balkan clade) and the newly discovered population, we compared 31 sequences from Slovakia and Hungary from Jablonski et al. (2019) together with four new from Albania and Slovakia (Suppl. material 1). A haplotype network was generated using PopArt (Leigh and Bryant 2015) (http://www.popart.otago.ac.nz) with the parsimony network algorithm (Clement et al. 2000), applying a 95% connection limit. Uncorrected *p* distances between native and introduced populations of *P. muralis* in Slovakia were calculated using DnaSP 6.00 (Rozas et al. 2017).

To determine whether the Danubian Lowland represents a suitable environment for *P. muralis* in Slovakia, we applied Species Distribution Modelling (SDM) using MaxEnt v.3.4.1 (Phillips et al. 2006) on a dataset of distribution data from native populations of the species in the country [own unpublished dataset of literature and Citizen Science data: aves.sk, biomonitoring.sk, GBIF.org (2024), iNaturalist.org (2024), nahuby.sk]. Model performance was assessed using the Area Under the Curve (AUC) metric, achieving a score of 0.93. We used 19 bioclimatic variables and elevation data at a 30-second resolution from the WorldClim database (Fick and Hijmans 2017), along with evaporation data (Trabucco et al. 2019) and range data

(Tuanmu and Jetz 2015). Based on correlation analysis and their influence on the species' model, we selected Bio2, Bio12, Bio15–17, Bio19, elevation, and evaporation. To address spatial autocorrelation, species occurrence data were pre-processed using the *SPThin* package in *R* 4.4.2 (RCoreTeam 2024). A minimum distance threshold of 5 km was applied, and 100 iterations were performed. The dataset was reduced from 269 records to 153. The SDMs used logistic output, 25% random test data, 10,000 background points, and ten replicates with cross-validation. All other settings were maintained at their default values.

To identify areas in Slovakia with environmental conditions similar to those in the lowlands of northern Albania and the southern part of Montenegro, we utilized a *Bash* script within GRASS GIS 8.2.0 on the Devana supercomputer to generate a Spatial Similarity Model (SSM). Our analysis prioritized biologically and ecologically significant variables while excluding redundant or less informative ones. To reduce redundancy in the dataset, we conducted a multicollinearity assessment and calculated the Variance Inflation Factor (VIF) using the *r.vif* module in GRASS GIS. Variables with VIF values exceeding 5 were excluded from further analysis (Marquardt, 1970). This resulted in a refined dataset of key climatic variables: Bio2, Bio8, Bio15, and Bio19. Additionally, we incorporated biologically significant predictors such as elevation, evapotranspiration, and range, which are critical for understanding ecological similarity among habitats. The resulting map highlights regions in Slovakia with environmental characteristics similar to the specified occurrence points within the target areas. These occurrence points were derived from datasets covering Albania, and Montenegro on the iNaturalist portal (2024). Map visualizations were created using QGIS 3.28 (2024; https://qgis.org/).

Results

Our two new sequences from Imeľ, Slovakia (965 bp), are nested in the phylogenetic tree alongside sequences from Austria (likely introduced populations near Vienna; see Jablonski et al. 2019), Bosnia and Herzegovina, Croatia, Greece, Slovenia, and with two newly provided sequences from northern Albania, forming distinct haplotypes with strong statistical support (Fig. 1A, B). Phylogenetically, this part of the tree corresponds to clades 11 and 12 sensu Salvi et al. (2013). These findings support the hypothesis of an "exotic" origin for the Imeľ population, as anticipated by the owner of the horticulture trade, who imports plants and materials from northern Albania. This represents the first genetically confirmed record of an introduced lineage of *P. muralis* in Slovakia, distanced 45 and 82 km from the closest genotyped localities of the species from Kováčov and Bratislava, respectively (Fig. 1C). The distinctness is also supported by the haplotype network analysis where Imeľ population is distanced by more than 43 mutations steps from other populations of the species representing the CB clade phylogeographically native to Slovakia. For the comparison, the uncorrected *p* distance between the haplotypes of the CB clade is from 1 to 4 mutation steps. The uncorrected *p* distance between the CB clade and Imeľ population is 4.6% (Fig. 1D). Both new sequences from Albania also support these results, with the sequence from Theth differing by only four mutation steps from those in Imeľ.

As confirmed by the SDM, the Danubian Lowland is generally not a suitable habitat for native populations of *P. muralis* belonging to the Central Balkan clade, except for its hilly part near Kováčov (Fig. 1C). According to the analysis, the most contributing bioclimatic variables were elevation (36.5%), Bio15 (Precipitation Seasonality; 29.7%), Bio16 (Precipitation of the Wettest Quarter; 8.8%), Bio19 (Precipitation of the Coldest Quarter; 7.9%), range (6.3%), and Bio17 (Precipitation of the Driest Quarter; 5.3%). Other variables, including evaporation, Bio2, and Bio12, contributed less than 5%. This suggests that the native populations from the Carpathian foothills are strongly influenced by altitudinal distribution and precipitation.

The SSM identified an area within the Danubian Lowland with similar environmental conditions (Fig. 1C), potentially suitable for the establishment of allochthonous populations of *P. muralis*. The model confirms that the region where the introduced population is currently present falls within this suitable area, suggesting it may support the reproduction and further spread of introduced *P. muralis*. However, this area is geographically limited but could potentially extend to overlap with native populations in the Kováčov region (Fig. 1C).

Discussion

We present the first evidence of an allochthonous population of *P. muralis* in Slovakia, likely introduced through stock and other horticultural materials from an unidentified region of northern Albania to a horticultural site in the Danubian Lowland. While unexpected in this specific geographical area, such introductions are not uncommon in the broader context of *P. muralis* (Schulte et al. 2008, 2011; Santos et al. 2019; Oskyrko et al. 2020; Kowalik et al. 2025) and other reptile species. Our observations indicate that the population is well-established and reproducing (juveniles reported also on autumn 2024, pers. obs.), which could pose an intriguing case for conservation genetics.

Hence, our results highlight several important points for further discussion. First, the role of international trade in natural goods, such as plants or soils, which can inadvertently introduce live specimens or eggs capable of establishing populations outside their native range, even in habitats with different climatic conditions. This is not an only introduction of *P. muralis* (Schulte et al. 2008, 2011; Santos et al. 2019; Kowalik et al. 2025) but the first confirmed record from the territory of Slovakia including Balkan population of lizards as a source which contrasts with western Europe where introductions come mostly from Apennine Peninsula (e.g. Michaelides et al. 2015). Globally introductions have been shown to significantly impact ecosystems (Soto et al. 2022). Thus, further genotyping of populations especially from Austria (Vienna is

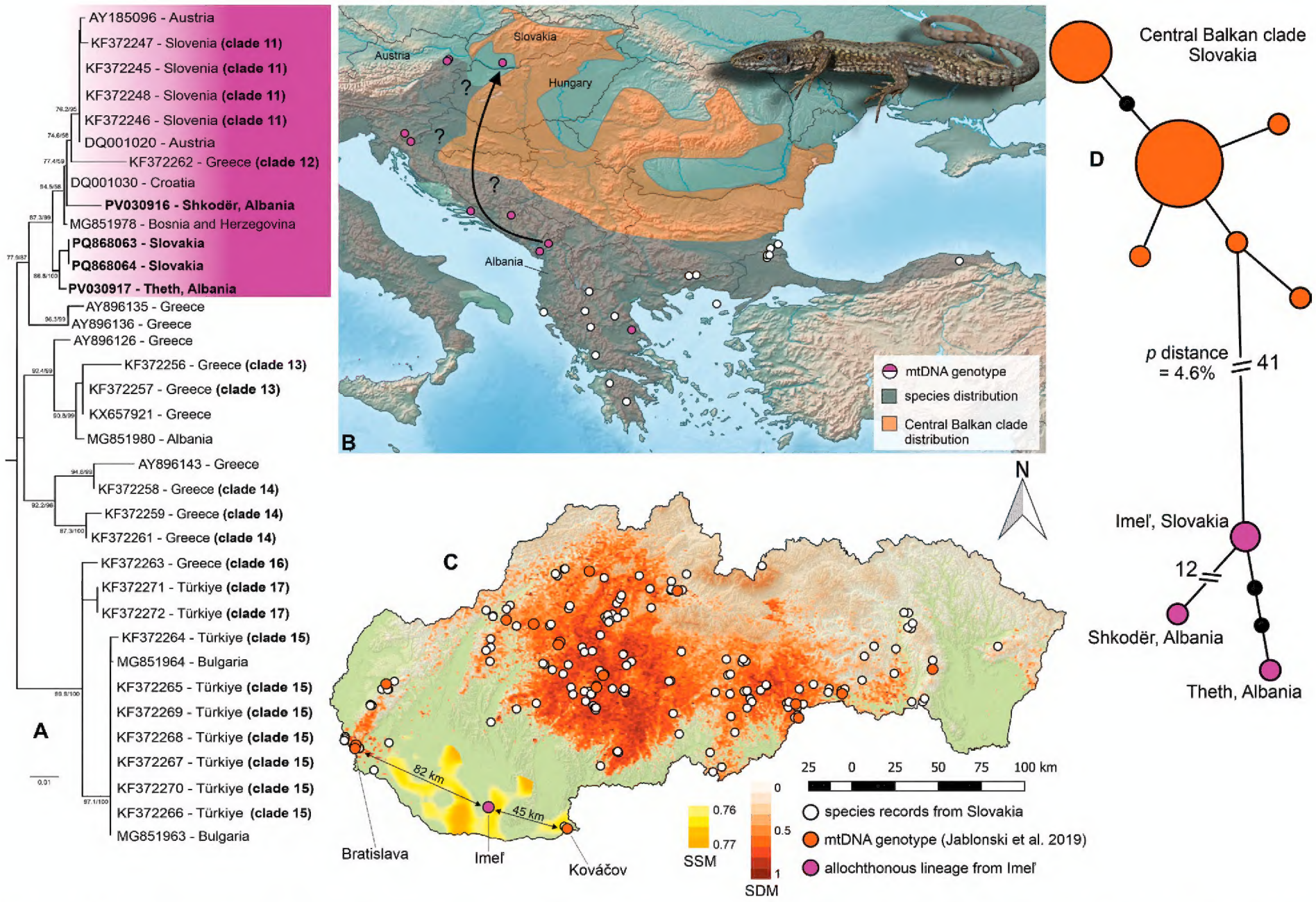

Figure 1. A. Maximum likelihood tree of Balkan *Podarcis muralis* populations from clades 11 to 17 (sensu Salvi et al. 2013), including the population from Imeľ, Slovakia and from northern Albania together with the species distribution context; **B.** The arrow indicates the possible origin of the Imeľ population from northern Albania, while the question mark highlights the area with the potential presence of the Central Balkan clade (see the orange range sensu Jablonski et al. 2019, Oskyrko et al. 2022); **C.** Distribution of the species in Slovakia, based on literature and citizen science data (own unpublished database; white dots), in the context of genotyped populations from Jablonski et al. (2019). Arrows represent the air distance (in km) to the closest genotyped populations with the native mtDNA genotype. The yellow layer represents the Spatial Similarity Model (SSM; above 0.76), which identifies areas in Slovakia that exhibit environmental conditions similar to those in lowlands of northern Albania or southern Montenegro. The orange layer represents the Species Distribution Model (SDM) for the species in Slovakia, where values above 0.5 indicate suitable habitats; **D.** Haplotype network includes Slovak populations from panel C and showing genetic distances between new and published sequences. The number between the orange and violet haplotypes indicates the number of mutational steps. The depicted individual is from the Imeľ population, Slovakia. Credit: Daniel Jablonski.

the type locality of the species), the Czech Republic, Hungary, and Slovakia may possibly discover lizards with an allochthonous origin that could have a potential impact on native populations or their ecological networks.

Second, such introductions would likely not have been successful without climate change. As confirmed by the SDM, *Podarcis muralis* in Slovakia is primarily distributed in hilly areas (Fig. 1C), often found around old castles or forest edges with moderate humidity (Lác et al. 2017). In contrast, the Danubian Lowland is not suitable for the presence of native populations according to the SDM but probably suitable for southern populations according to the SSM. In Albania, *P. muralis* is a common species occurring from sea level to high mountains (Mizsei et al. 2017; Jablonski, pers. obs.), thriving across a wide range of ecological and climatic conditions. The conditions, however, changed in the past 20 years in the Danubian Lowland which may allow the establishment of allochthonous populations of the species from the Mediterranean area. The southern part of Slovakia, specifically the Danubian Lowland, ranks among the warmest regions in the country. The vegetation period lasts on average 200 days with an average temperature of 17.9 °C, with July and August being the hottest months. In recent decades, the influence of climate change has become evident, manifesting in the rising average annual temperature. At the meteorological station in Hurbanovo in the Danubian Lowland (data of Slovak Hydrometeorological Institute), the average temperature from 1991 to 2023 was 11.2 °C, which further increased to 11.5 °C after 2000. Significant changes have also been observed in maximum temperatures, with temperatures above 38 °C recorded multiple times, the highest being 40.3 °C in 2007. On the other hand, winters have become milder, with a 36% reduction in days with temperatures below -10 °C, and the average minimum temperatures have also moderated in recent years. The exceptionally above-average temperature in February 2024 was reflected in the highest monthly average air

temperature in the southwest of the territory (Hurbanovo 9.1 °C). This trend illustrates the possible warming of the region and changes in temperature and precipitation patterns that could provide conditions for establishing populations of animals from southern parts of Europe.

Third, the presence of introduced populations of *P. muralis* poses potential risks as they may serve as sources of genetic admixture with local populations, which could further expand as partly suggest the SSM (potential contact in the region of Kováčov; Fig. 1C). This issue is particularly concerning given that *P. muralis* is a protected species in Slovakia, and under existing legislation, even introduced populations are granted protection based on their species status. However, the newly discovered population is not native and has a distinct evolutionary history compared to the CB clade found in this region of Europe (Fig. 1B). Fortunately, the introduced population, although reproducing, is currently small and situated several dozen kilometres away from native populations in Bratislava and Kováčov, near the Slovak-Hungarian border.

Our results open further space for research on native reptile populations by combining distribution and genetic data. This can provide a deeper understanding of the dynamics of allochthonous *P. muralis* in the region and its potential impact on native species. Therefore, it is crucial to monitor the presence of *P. muralis* in other areas of the Danubian Lowland and the wider Pannonian Basin and genotype these populations to study their genetic affiliation and possible admixture. Ongoing surveillance, involving citizen science efforts, will help determine the extent of the population's spread, particularly in areas where it may pose a risk to native species. Further monitoring, in collaboration with local research and conservation authorities, is necessary to assess the implications of these findings for ongoing efforts (e.g., controlling the spread in sensitive habitats, engaging the public through education and citizen science initiatives) to protect local genetic diversity.

Acknowledgments

We would like to thank Zoltán Lovász, the landowner on whose property the studied population was located, for kindly allowing us unrestricted access. We also extend our gratitude to Jana Poláková for her assistance in the DNA laboratory, Dominik Zerzán for providing tissue samples, and three anonymous reviewers for their constructive and valuable comments on the first submitted version. Supported by the EU NextGenerationEU scholarship through the Recovery and Resilience Plan of the Slovak Republic within the project no. 09I03-03-V04-00306.

References

Allan GM, Prelypchan CJ, Gregory PT (2006) Population profile of an introduced species, the common wall lizard (*Podarcis muralis*), on Vancouver Island, Canada. Canadian Journal of Zoology 84: 51–57. https://doi.org/10.1139/z05-176

Clement M, Posada D, Crandall, KA (2000) TCS: A computer program to estimate gene genealogies. Molecular Ecology 9: 1657–1659. https://doi.org/10.1046/j.1365-294x.2000.01020.x

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37: 4302–4315. https://doi.org/10.1002/joc.5086

Funk A, Vlček P (2023) Cesta dlážděná dobrými úmysly aneb „Šíření" ještěrky zední a rizika nepůvodních populace [A Road Paved by Good Intentions: the „Spread" of the Common Wall Lizard and the Risk to Non-native Populations]. ŽIVA 71 (109): 198–201. [in Czech]

GBIF.org [15 January 2024] (2024) GBIF Occurrence Download. https://doi.org/10.15468/dl.ze7f7q

GRASS Development Team (2022) Geographic Resources Analysis Support System (GRASS) Software, Version 8.2. Open Source Geospatial Foundation. Electronic document. https://doi.org/10.5281/zenodo.5176030

Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. Systematic Biology 59: 307–321. https://doi.org/10.1093/sysbio/syq010

iNaturalist (2024) Observations of taxon: *Podarcis muralis*. https://www.inaturalist.org/observations?taxon_id=55990 [Accessed 31 December 2024]

Jablonski D, Gvoždík, V, Choleva L, Jandzik D, Moravec J, Mačát Z, Veselý M (2019) Tracing the maternal origin of the common wall lizard (*Podarcis muralis*) on the northern range margin in Central Europe. Mitochondrion 46: 149–157. https://doi.org/10.1016/j.mito.2018.04.006

QGIS 3.28 (2024) [Development Team] (2024) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.org [accessed 12 July 2024]

Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. Nature Methods 14: 587–589. https://doi.org/10.1038/nmeth.4285

Kolenda K, Skawiński T, Majtyka M, Kuśmierek N, Starzecka A, Jablonski D (2020) Biology and origin of isolated north-easternmost population of the common wall lizard, *Podarcis muralis*. Amphibia-Reptilia 41: 429–443. https://doi.org/10.1163/15685381-bja10011

Kowalik C, Skawiński T, Boesl D, Celiński D, Jablonski D, Kolenda K (2025) Tracking the origin and current distribution of wall lizards (*Podarcis* spp.) in Poland. Amphibia-Reptilia 46: 69–83. https://doi.org/10.1163/15685381-bja10206

Lác J (1970) Poznatky o rozšírení a ekológii jašterice múrovej stredoeurópskej (*Lacerta muralis muralis* Laur.) na Slovensku. Ochrana fauny 4(3): 106–111. [in Slovak]

Lác J, Kautman J, Zavadil V (2017) Plazy Slovenska, faunisticko – ekologická štúdia. Nepublikovaný, komentovaný rukopis. [Reptiles of Slovakia, faunistic – ecological study. Unpublished, annotated manuscript]. Acta Rerum Naturalium Musei Nationalis Slovaci 63: 44–110. [in Slovak]

Leigh JW, Bryant D (2015) Popart: Full-feature software for haplotype network construction. Methods in Ecology and Evololution 6: 1110–1116. https://doi.org/10.1111/2041-210X.12410

Marquardt DW (1970 Generalized inverses, ridge regression, biased linear estimation, and nonlinear estimation. Technometrics 12: 591–612. https://doi.org/10.2307/1267205

Michaelides SN, While GM, Zajac N, Uller T (2015) Widespread primary, but geographically restricted secondary, human introductions

of wall lizards, *Podarcis muralis*. Molecular Ecology 24: 2702–2714. https://doi.org/10.1111/mec.13206

Minh BQ, Nguyen MAT, von Haeseler A (2013) Ultrafast approximation for phylogenetic bootstrap. Molecular Biology and Evolution 30: 1188–1195. https://doi.org/10.1093/molbev/mst024

Mizsei E, Jablonski D, Végvári Z, Lengyel S, Szabolcs M (2017) Distribution and diversity of reptiles in Albania: a novel database from a Mediterranean hotspot. Amphibia-Reptilia 38: 157–173. https://doi.org/10.1163/15685381-00003097

Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular Biology and Evolution 32: 268–274. https://doi.org/10.1093/molbev/msu300

Oskyrko O, Sos T, Vacheva E, Vlad SE, Cogălniceanu D, Uller T, Feiner N, Carretero MA (2022) Unravelling the origin of the common wall lizards (*Podarcis muralis*) in south-eastern Europe using mitochondrial evidence. Biodiversity Data Journal 10: e90337. https://doi.org/10.3897/BDJ.10.e90337

Oskyrko O, Laakkonen H, Silva-Rocha I, Jablonski D, Marushchak O, Uller T, Carretero MA (2020) The possible origin of the common wall lizards, *Podarcis muralis* (Laurenti, 1768) in Ukraine. Herpetozoa 33: 87–93. https://doi.org/10.3897/herpetozoa.33.e49683

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distribution. Ecological Modelling 19: 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

RCoreTeam (2024) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org [accessed on 31 October 2024]

Rozas J, Ferrer-Mata A, Sánchez-DelBarrio JC, Guirao-Rico S, Librado P, Ramos-Onsins S.E, Sánchez-Gracia A (2017) DnaSP 6: DNA sequence polymorphism analysis of large datasets. Molecular Biology and Evolution 34: 3299–3302. https://doi.org/10.1093/molbev/msx248

Santos JL, Žagar A, Drašler K, Rato C, Ayres C, Harris DJ, Carretero MA, Salvi D (2019) Phylogeographic evidence for multiple long-distance introductions of the common wall lizard associated with human trade and transport. Amphibia-Reptilia 40: 121–127. https://doi.org/10.1163/15685381-20181040

Salvi D, Harris DJ, Kaliontzopoulou A, Carretero MA, Pinho C (2013) Persistence across Pleistocene ice ages in Mediterranean and extra-Mediterranean refugia: phylogeographic insights from the common wall lizard. BMC Evolutionary Biology 13: 147. https://doi.org/10.1186/1471-2148-13-147

Schulte U, Bidinger K, Deichsel G, Hochkirch A, Thiesmeier B, Veith M (2011) Verbreitung, geografische Herkunft und naturschutzrechtliche Aspekte allochthoner Vorkommen der Mauereidechse (*Podarcis muralis*) in Deutschland. Zeitschrift für Feldherpetologie 18: 161–180.

Schulte U, Hochkirch A, Loetters S, Roedder D, Schweiger S, Weimann T, Veith M (2012) Cryptic niche conservatism among evolutionary lineages of an invasive lizard. Global Ecology and Biogeography 21: 198–211. https://doi.org/10.1111/j.1466-8238.2011.00665.x

Schulte U, Thiesmeier B, Mayer W, Schweiger S (2008) Allochthone Vorkommen der Mauereidechse (*Podarcis muralis*) in Deutschland. Zeitschrift für Feldherpetologie 15: 139–156.

Soto I, Cuthbert RN, Kouba A, Capinha C, Turbelin A, Hudgins EJ, Diagne C, Courchamp F, Haubrock PJ (2022) Global economic costs of herpetofauna invasions. Scientific Reports 12: 10829. https://doi.org/10.1038/s41598-022-15079-9

Speybroeck J, Beukema W, Bok B, Van Der Voort J (2016) Field guide to the amphibians and reptiles of Britain and Europe. Bloomsbury, London, UK, 432 pp.

Trabucco A, Zomer R (2019) Global Aridity Index and Potential Evapotranspiration (ET0) Climate Database v2. Figshare. Fileset. https://doi.org/10.6084/m9.figshare.7504448.v3

Tuanmu M.-N., Jetz W (2015) A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modeling. Global Ecology and Biogeography 24: 1329–1339. https://doi.org/10.1111/geb.12365

Trifinopoulos J, Nguyen LT, von Haeseler A, Minh BQ (2016) W-IQ-TREE: A fast online phylogenetic tool for maximum likelihood analysis. Nucleic Acids Research 44: W232–W235. https://doi.org/10.1093/nar/gkw256

Wirga M, Majtyka T (2015) Do climatic requirements explain the northern range of European reptiles? Common wall lizard *Podarcis muralis* (Laur.) (Squamata, Lacertidae) as an example. North-Western Journal of Zoology 11: 296–303.

Yang W, Feiner N, Salvi D, Laakkonen H, Jablonski D, Pinho C, Carretero MA, Sacchi R, Zuffi MAL, Scali S, Plavos K, Pafilis P, Poulakakis N, Lymberakis P, Jandzik D, Schulte U, Aubret F, Badiane A, Perez I de Lanuza G, Abalos J, While GM, Uller T (2022) Population genomics of wall lizards reflects the dynamic history of the Mediterranean Basin. Molecular Biology and Evolution 39: msab311. https://doi.org/10.1093/molbev/msab311

Supplementary material 1

Sequences used in the phylogenetic analysis

Authors: Daniel Jablonski, Martin Raffaj, Dušan Senko
Data type: docx
Explanation note: A - Dataset for for the tree analysis. B - Dataset for the haplotype network analysis.
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/herpetozoa.38.e139307.suppl1